

**SUPERSPECIES *ATRYTONOPSIS OVINIA* (*A. OVINIA* PLUS
A. EDWARDSI) AND THE NONADAPTIVE NATURE OF
INTERSPECIFIC GENITALIC DIFFERENCES
(LEPIDOPTERA: HESPERIIDAE)**

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Abstract.—Superspecies *Atrytonopsis ovinia* comprises *A. ovinia* (Nicaragua to central Mexico) and *A. edwardsi* (central Mexico to Texas and Arizona); *zaovinia* is a synonym of *ovinia*; *rupilius*, a *nomen dubium*. Characters of size, antenna, sex behavior, stigma, facies, genitalia, and temporal and spatial distribution define this superspecies; the most distinctive are wing shape and genital characters involving the uncus, aedeagus, and ductus bursae. Wing length and number of segments in the nudum of the antenna vary independently; the former is sexually dimorphic, but the latter is not. (Sexual dimorphism in wing length is greater in *A. edwardsi* than it is in *A. lunus*, even though *lunus* is the larger species.) Those morphologic characters that best separate *ovinia* from *edwardsi* are secondary sex characters: the stigma and some subtle differences in male (uncus) and female (lamella postvaginalis) genitalia. In each of these allopatric and discontinuously distributed species, these (and other) characters show lots of individual—but not geographic—variation. The slight genitalic differences between *ovinia* and *edwardsi* give no evidence of having been directly selected. Such taxonomically useful differences may often be nonadaptive. The data support a punctuational model of speciation.

Atrytonopsis is a compact genus of a dozen species centered in the southwestern United States and Mexico. North of Mexico, it does not approach the West Coast, though it spreads clear to the East Coast via *hianna* (Scudder), which stretches northward to southeastern Saskatchewan and New England, and *loammi* (Whitney), which replaces *hianna* mainly in Florida. Defined by Godman in 1900 with *Hesperia deva* Edwards as its type, *Atrytonopsis* has a distinctive shape that stems primarily from the pointed forewings of males.

I started reviewing *Atrytonopsis* when I saw that *Lychnuchoides frappenda* Dyar must be switched to it. This seemingly big shift, from Evans' (1955) K or *Carystus* Group to his N or *Lerodea* Group, significantly extended the range of variation in facies (though not in genitalic or other morphology) of *Atrytonopsis* (Burns, 1982). *Atrytonopsis frappenda* clusters tightly with *lunus* (Edwards) and *zweifeli* Freeman to form the *lunus* group, a trio of species that looks, from limited locality data, like a superspecies occurring from southeastern Arizona and southwestern New Mexico to central Mexico. I now delimit superspecies *A. ovinia* whose com-

ponents have not been correctly handled. They come down to a pair of species that stands out both externally (the primaries are more rounded than they are in other species of *Atrytonopsis*) and internally (the genitalia deviate from the *Atrytonopsis* norm, most notably in the form of the uncus and the length of the aedeagus and ductus bursae). This is the southmost group in the genus.

As with the *lunus* group, so with superspecies *A. ovinia*: with an eye to variation, I take up characters (rather than taxa) seriatim, using each, first, to define the superspecies *ovinia* within genus *Atrytonopsis* and then, when pertinent, to distinguish between the two component species. However, I have to begin by establishing correct names for these species; supporting evidence (including critical illustrations of type-specimens) comes after.

SUPERSPECIES *ATRYTONOPSIS OVINIA*

Nomenclature and synonymy.—*Hesperia ovinia* Hewitson (1866: 496) from Nicaragua was the first species of what is now *Atrytonopsis* to be described. Although most species had surfaced by 1900 when Godman created the genus, all of the names besides *ovinia* relating to superspecies *ovinia* appeared in a flurry in the second decade of this century: *Thespieus zaovinia* Dyar (1913: 280) from Tehuacan, Mexico; *Lerodea? rupilius* Schaus (1913: 360) from Guapiles, Costa Rica; and *A. edwardsi* Barnes and McDunnough (1916: 135) from southern Arizona. With types of all three at hand in the National Museum of Natural History (USNM), I had only to get that of *ovinia* from the British Museum (Natural History) to compare all relevant type-material directly.

Barnes and McDunnough (1916: 135 and pl. 8, figs. 9 and 10) described *edwardsi* when they realized that it was an anonymous species "passing under the name of *cestus*" (Edwards), a much rarer *Atrytonopsis* from southern Arizona. Soon after, Lindsey (1921: 95) said:

I believe that the name [*edwardsi*] will fall before *Hesperia ovinia* Hew., illustrated in the *Biologia* (Pl. 97, ff. 1, 2, 1900) under the name *Thespieus ovinia*. The type of *ovinia* in the British Museum will have to be examined to settle the matter definitely, but even from the figures it is easy to see that the species can hardly belong in *Thespieus*.

A decade later Lindsey et al. (1931: 122) noted:

The relationship of this species [*edwardsi*] and *ovinia* Hewitson which was mentioned in the first edition of this work is still unsettled.

And so it remained, even after Evans (1955: 385-386), who had seen the type of *ovinia* (but not those of *zaovinia*, *rupilius*, and *edwardsi*), treated *A. ovinia* as a polytypic species with the two subspecies *ovinia* and *zaovinia* and made *rupilius* and *edwardsi* synonyms of *zaovinia*. His arrangement has always struck me as geographically and biologically anomalous: one subspecies (*ovinia ovinia*) in Nicaragua and the other (*ovinia zaovinia*) both to the north in Mexico plus the southwestern United States and to the south in Costa Rica. The combination *A. ovinia edwardsi* in dos Passos' (1964: 5) checklist was introduced by dos Passos (1960: 28) in anticipation of that list and "justified" as follows:

Examination of specimens in the American Museum of Natural History collection shows that *edwardsi* is entitled to subspecific rank.

This combination has persisted in important works to the present (MacNeill, 1975: 445; Miller and Brown, 1981: 47). It is not far off the mark. But *edwardsi* is really a separate species from *ovinia*. And *zaovinia*, which has persisted since 1913 as a species (e.g., Hoffmann, 1941: 274) or subspecies (e.g., Evans, 1955: 386; Okano, 1981: 111), is a synonym of *ovinia*. At the end of his original description of *zaovinia* Dyar (1913: 281) said:

This species is close to *T. ovinia* Hewitson, but the subapical spots of the fore wing are not in line and the spots on the hind wing below are narrow.

These purported specific differences amount to nothing more than routine individual variation.

Using a good color figure of dorsal and ventral aspect as well as words, Schaus (1913: 360 and pl. 54, fig. 10) described *rupilius* from a single female from Guapiles, Costa Rica. But what masquerades as the type of *rupilius* is a female labelled "Guadjara/Mex" which, though very similar in general to the Schaus color figure, actually differs from it in many details. There is no trace of the lady from Guapiles. Were she around, her genitalia would probably fit the *ovinia* mold. As it is, the genitalia of the substitute from Guadalajara belong to *edwardsi*. Because the name *rupilius* cannot be unequivocally tied to a taxon, it becomes a *nomen dubium* and evades synonymy.

At this point, a tangent on type-localities is in order. Hewitson (1866: 496), in his original description, gave the source of *ovinia* as Nicaragua. Both Godman (1900: 521) and Evans (1955: 386) indicated that the three specimens of *ovinia* in BMNH, which include Hewitson's, are from Nicaragua; and Evans also noted specifically that the male type is from Nicaragua. Having borrowed all three specimens, including the type, I have seen their Nicaragua labels for myself. Miller and Brown (1981: 47) erroneously give the type-locality of *ovinia* as "Venezuela."

Barnes and McDunnough (1916: 135) described *edwardsi* from seven dateless specimens (all in USNM) from southern Arizona: 3 ♂ 1 ♀ with no further locality data, 2 ♀ from the Baboquivari Mountains, and 1 ♂ from Redington. The text accompanying the original description, as well as labels on the specimens themselves, clearly designate the Redington male as Type ♂, one of the Baboquivari females as Type ♀, and all other specimens as Paratype ♂ or ♀. To avoid any possible confusion, I am designating the "Type ♂" lectotype. Although the restricted type-locality, "Redington, Arizona," is ecologically out-of-bounds for *edwardsi*, it is eminently reasonable to construe "Redington" as higher ground to the west, to wit, the "Santa Catalina Mountains."

Much of the foregoing may be summarized thus:

Superspecies *Atrytonopsis ovinia*

A. ovinia (Hewitson), 1866, [*Hesperia*], Nicaragua, holotype ♂, BMNH.
= *zaovinia* (Dyar), 1913, [*Thespieus*], Tehuacan, Mexico, holotype ♂, USNM.

A. edwardsi Barnes and McDunnough, 1916, Redington (→ Santa Catalina Mountains), Arizona, lectotype ♂, USNM.

Nomen dubium: *rupilius* (Schaus), 1913, [*Lerodea?*], Guapiles, Costa Rica, holotype ♀ missing; substituted phony "type" ♀, Guadalajara, Mexico, USNM.

Size.—With male forewings averaging about 18 mm (Table 1), both members of superspecies *A. ovinia* occupy the upper middle size range of *Atrytonopsis*.

Table 1. Length (mm) of right primary in superspecies *Atrytonopsis ovinia*.

Sample	Sex	N	Range	Mean with Standard Error	Standard Deviation	Coefficient of Variation
<i>A. edwardsi</i>						
Arizona						
Santa Catalina Mountains	♂	40	16.5–19.4	17.89 ± 0.11	0.67	3.75
	♀	11	17.9–21.3	19.45 ± 0.36	1.20	6.17
Baboquivari Mountains	♂	52	16.0–20.2	17.93 ± 0.12	0.85	4.74
	♀	33	17.8–20.7	19.41 ± 0.14	0.80	4.12
Texas						
Davis Mountains	♂	28	16.7–19.8	18.09 ± 0.14	0.73	4.04
	♀	15	18.4–20.6	19.41 ± 0.19	0.73	3.76
<i>A. ovinia</i>						
Mexico						
Puebla, Guerrero, Oaxaca,	♂	23	17.0–20.6	18.23 ± 0.19	0.90	4.94
	♀	8	18.1–19.4	18.79 ± 0.14	0.39	2.08
Tabasco, Chiapas	♂	2	20.1–20.4			
	♀	1	20.6			

Sexual dimorphism appears strong in *edwardsi* (though not in *ovinia*, probably owing to sampling error). Indeed, sexual dimorphism is greater in *edwardsi* than it is in *lunus*, even though *lunus* is the larger species: *lunus* males average about 21 mm in wing length and *lunus* females, nearly 1 mm more (Burns, 1982: 549); *edwardsi* males average about 18 mm but *edwardsi* females, about 1½ mm more (Table 1). In all three samples of *edwardsi*, the difference in mean size between males and females is highly significant.

Within each sex, there are no significant differences in size among samples of *edwardsi*. In other words, *edwardsi* seems not to vary geographically in size (at least within the United States).

Nor are there really significant size differences, in either sex, between *edwardsi* and *ovinia*, although, to judge from males (which afford the better sample), *ovinia* may be a trifle larger.

All wing measurements were taken twice (see Burns, 1982: 549).

Antenna.—In true dorsal view, the posterior side of the base of the club is more noticeably pale in superspecies *A. ovinia* than it is in other *Atrytonopsis*.

On average, the apiculus is longer in superspecies *A. ovinia* than it is in any of the other *Atrytonopsis* that usually or always have spots on the dorsal secondary. It looks at least as long as it does in the *lunus* group, which has the longest apiculus among species of *Atrytonopsis* that normally lack spots on the dorsal secondary. Yet the apiculus averages 0.7 segment less in superspecies *A. ovinia* than it does in the *lunus* group. This is manifest when one compares *lunus* and *edwardsi* from Arizona, where samples are large; but limited data from elsewhere suggest a similar difference.

Variation in number of segments in the nudum is demonstrably independent of variation in size: although females of *edwardsi* average significantly larger than males in wing length (Table 1), they do not differ from males in number (and

Table 2. Frequency (%) of nudum variants in males vs. females of *Atrytonopsis edwardsi* from mountain islands in southern Arizona.

Sample	Sex	N	Number of Nudum Segments (on Base of Club/on Apiculus)						
			4/6	3/7	3/8	4/7	4/8	4/9	5/8
Santa Catalina Mountains	♂	43		1 (2)	4 (9)	8 (19)	27 (63)	2 (5)	1 (2)
	♀	11			1 (9)	2 (18)	7 (64)	1 (9)	
Baboquivari Mountains	♂	80	1 (1)	2 (3)	1 (1)	12 (15)	56 (70)	6 (7)	2 (3)
	♀	40		1 (3)		5 (13)	29 (72)	2 (5)	3 (7)

disposition) of nudum segments (Table 2). I previously found ample sexual dimorphism in size but none in expression of the nudum in *lunus* (Burns, 1982: 551) and in *Erynnis propertius* (Scudder and Burgess) (Burns, 1964: 97, table 14); the data, particularly for *Atrytonopsis*, were fragmentary. Using scattered data from *Erynnis*, I argued once before that wing length and number of nudum segments must vary independently (Burns, 1964: 10).

Nudum variation in superspecies *A. ovinia* is summarized in Table 3, where data from both sexes are pooled. Except for 8 individuals (out of a total of 251 scored), the number of nudum segments surpasses the 10 (disposed 4/6) that Evans (1955: 384) attributed to genus *Atrytonopsis*. Ranging from 10 to 13, the number of segments is usually 11 or 12 in *ovinia* (disposed 4/7 or 4/8) and 12 in *edwardsi* (disposed 4/8). In *lunus*, the number ranges from 11 to 15 and is usually 12, 13, or 14 (disposed 4/8, 5/8, 4/9, or 5/9) (Burns, 1982: 550). As in the *lunus* group, the terminal segment is almost always long.

Clearly, the nudum (which includes the apiculus) is slightly shorter, on average, in *ovinia* from Mexico than it is in *edwardsi* from the United States (Table 3). However, in the few specimens of *edwardsi* I have seen from far down in Mexico (2 from Jalisco, 1 from Veracruz), where they approach the northern limit of *ovinia*, the nudum is 4/7; and in the only specimen of *ovinia* from Nicaragua with an unbroken antenna, the nudum is 4/9.

Though there may be modest geographic variation in the nudum of *edwardsi* between southern Arizona and west Texas, the Davis Mountains sample may be relatively conservative chiefly because 38 of the 43 specimens in it were taken (by my wife and me) in a 1-week period—35 of them from a single local population. Other samples come from many times and populations. Some of the variation in the phenotype of the nudum no doubt reflects "environmental slop," such as differences in weather at critical developmental times.

Sex ratio and behavior.—Although, as a rule, the sex ratio is probably about even in natural populations of skippers, it seldom is in collected material. There the number of males commonly exceeds the number of females—often by 2 (or more) to 1. Both *edwardsi* and *ovinia* fit this pattern (see Tables 1 and 2). But, because *lunus* and *frappenda* completely reverse it (Burns, 1982: 549), I infer important behavioral differences between superspecies *A. ovinia* and the *lunus* group.

Stigma.—The stigma of *Atrytonopsis* extends narrowly and obliquely across the forewing from the middle of vein 1 to about the origin of vein 3. It is tripartite owing to characteristic interruptions in space 1b and at vein 2.

Table 3. Frequency of nudum variants in superspecies *Atrytonopsis ovinia*.

Sample	N	Number of Nudum Segments (on Base of Club/on Apiculus)								
		4/6	3/7	3/8	4/7	5/7	4/8	4/9	5/8	
<i>A. edwardsi</i>										
Arizona										
Santa Catalina Mountains	54		1	5	10		34	3	1	
Baboquivari Mountains	120	1	3	1	17		85	8	5	
Texas										
Davis Mountains	43				1	1	37	2	2	
<i>A. ovinia</i>										
Southern Mexico	21	2	1		9		9			

For a hesperiine stigma, it is weak. It almost appears to be losing its evolutionary grip: totally lacking in the *lunus* group, it runs the gamut from all to nothing in *deva*, and varies considerably in expression in other species (Burns, 1982: 551). The stigma is as well developed in superspecies *A. ovinia* as it is in any *Atrytonopsis*: I have seen only one male of *ovinia* and one of *edwardsi* in which it is extremely reduced.

The stigma offers the best means of distinguishing (males of) *ovinia* from (males of) *edwardsi*.

In *ovinia* (Figs. 1–5), it is exceedingly narrow but relatively conspicuous because the fine scales that form it are pale enough to contrast sharply with the coarser, dark brown scales all around. It makes a steep, high angle with vein 1. The entire stigma is often straight enough to suggest a ruled broken line. The upper part of it terminates mediad of the medial edge of the spot in space 2—usually at some point roughly equidistant between this spot and the spot in the cell.

By contrast, the stigma of *edwardsi* (Figs. 6–10) is broad but relatively hard to see because it is darker and tends to blend with the surrounding ground. Its upper part is less well aligned with the middle and lower parts and is directed more outward than it is in *ovinia* so that the stigma as a whole makes a lower angle with vein 1. The upper part of the stigma terminates at the medial edge of the spot in space 2. Along the cubital vein immediately above the upper part of the stigma, many coarse scales are raised and turned abruptly downward toward it. The overall result is the most elaborate stigma in the genus. (Such altered scales on the cubitus are missing to, at most, moderately developed in *ovinia*.)

These differences hold through the geographic range of both species.

Facies.—Wings are more rounded in superspecies *A. ovinia* than they are in other *Atrytonopsis*. This is particularly evident in the forewings of males.

Both species of superspecies *A. ovinia* have a bold spot spanning the cell of the primary and at least some spots on the dorsal secondary (Figs. 11–18). In general, the row of spots on the dorsal secondary is not as hypertrophied as it is in *cestus*, not as continuous and straight as it is in *pittacus* (Edwards), but not as uneven as it is in *python* (Edwards) and *margarita* (Skinner).

Fringes of both wings are checkered (rather more clearly in *edwardsi* than in *ovinia*), though not as strongly as they are in *python*.

The gap between the large semihyaline spot in space 2 and the one in the cell is generally a little smaller in *ovinia* than it is in *edwardsi* (Figs. 1–18). This is true especially of males, owing to differences in the form and position of the upper part of the stigma (described above).

On average, the row of spots on the dorsal secondary is slightly less developed and slightly more even in *ovinia* than it is in *edwardsi*. (Comparisons must be made *within* each sex because, in *Atrytonopsis*, this row of spots is better developed, on average, in males than it is in females.) The spots themselves are ever so slightly more rounded in *edwardsi* than they are in *ovinia*.

Genitalia.—Although the genitalia of *Atrytonopsis* are conservative, those of superspecies *A. ovinia* depart relatively widely from the rest. Within the superspecies, however, specific differences are slight and tend to be blurred by a healthy lot of individual variation.

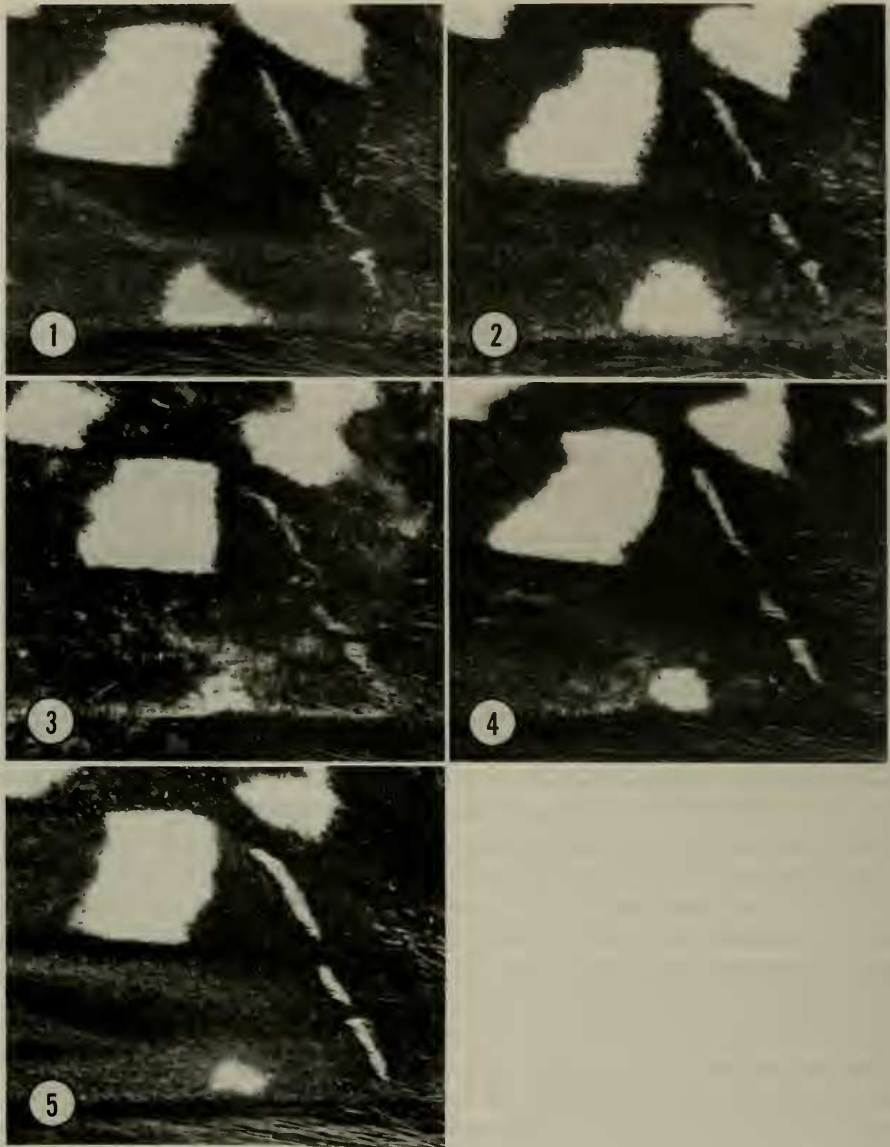
Accordingly, numerous genitalia have been dissected, compared, and stored in 1-dram vials that leave them fully liberated (for procedural details, see Burns, 1982: 557). As before, dissection numbers of drawn individuals appear in figure legends in parentheses.

Male genitalia: The paired uncus prongs, which are long and narrow in all other *Atrytonopsis*, are fused for most of their length and separate only at their tips in superspecies *A. ovinia* (Figs. 19, 22, 25, 28–40). The aedeagus, which is always long in *Atrytonopsis*, is excessively long in superspecies *A. ovinia*—nearly thrice the length of the valva (Figs. 20–21, 23–24, 26–27).

The small notch dividing the tip of the uncus is always a little deeper in *ovinia* than it is in *edwardsi* (cf. Figs. 19, 22, 28–33 with 25, 34–40). The two states of this character are so similar that it is hard to choose between them without seeing both at once. What is worse, both states vary considerably (as Figs. 19, 22, 25, 28–40 try to show). Nevertheless, they do not overlap: the notch between the uncus prongs is decidedly deeper than the basal diameter of either prong in *ovinia* but more or less equal to (or even shallower than) the basal diameter of either prong in *edwardsi*. Another beauty of this subtle character is its location at the distal end of the genitalia where it can often be studied—without having to dissect—by, at most, brushing away a few scales.

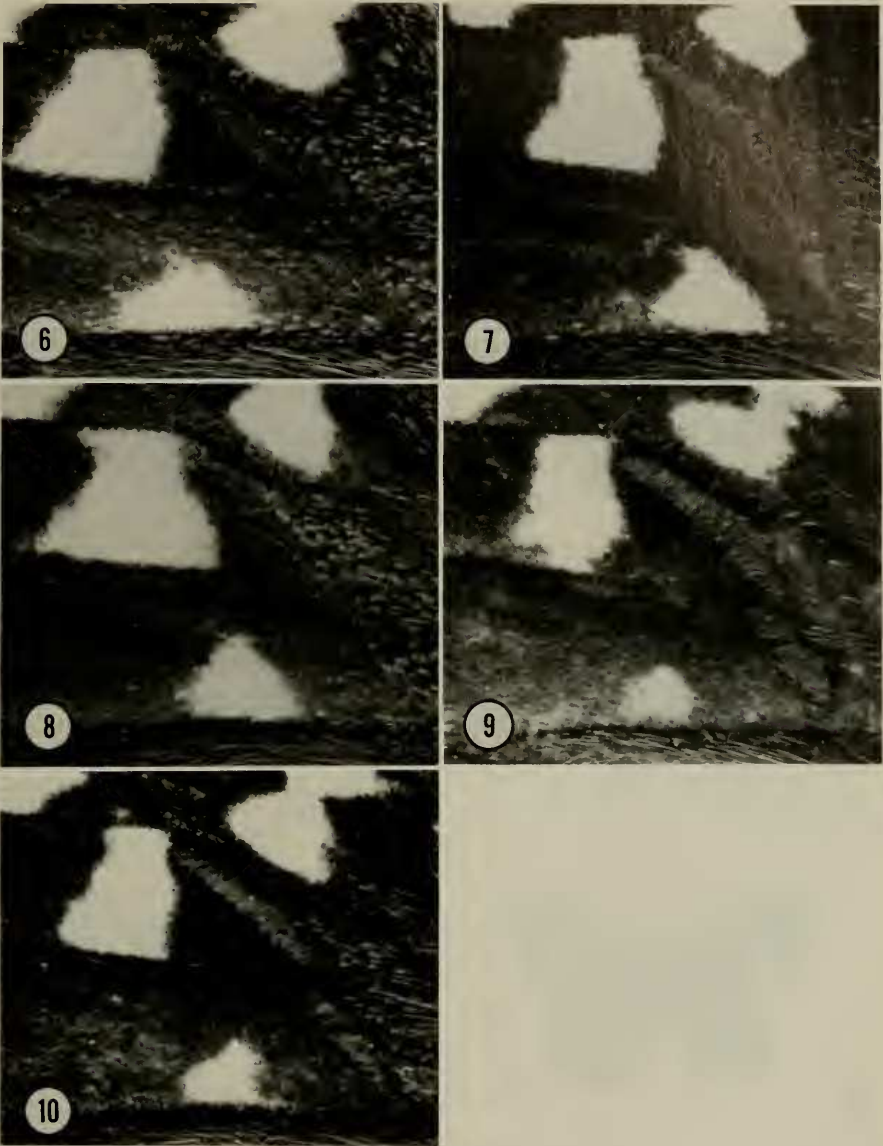
Female genitalia: The lamella postvaginalis is more elongate and more narrowly stalked in superspecies *A. ovinia* than it is in other *Atrytonopsis* (Figs. 41–55). The ventral lip of the ostium bursae is peculiar because it begins at the sides in large, sclerotized, caudally projecting points from which it arcs somewhat forward, giving way midventrally to an area of membrane that gradually and irregularly becomes sclerotized a little farther forward (Figs. 41–55). As in other *Atrytonopsis*, the ductus bursae is heavily sclerotized (Burns, 1982: 562); but it is much longer in superspecies *A. ovinia* than it is in other members of the genus. (In view of the excessively long aedeagus of the corresponding males and the fashionability of coevolution, this comes as no surprise.) At first elliptical to round in cross section, the ductus bursae flattens anteriorly and, before emptying into the corpus bursae, bends to the right in a characteristic way (Figs. 41–55).

Although the lamella postvaginalis is very similar in *ovinia* and *edwardsi* and varies greatly in form within each species (Figs. 41–55), it will serve to distinguish them unequivocally. Seen ventrally, the lamella postvaginalis is essentially lanceolate (with a rounded apex) in *ovinia* but deltoid in *edwardsi*. In *ovinia*, it is



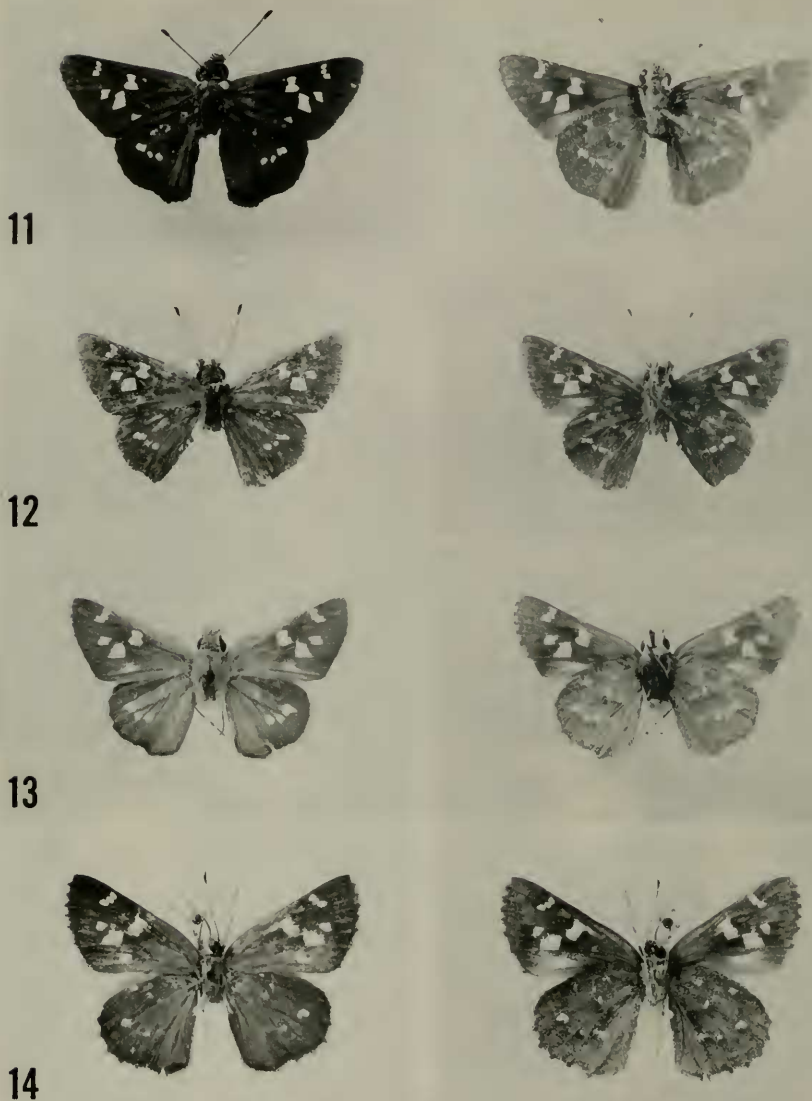
Figs. 1-5. Male stigmas of *Atrytonopsis ovinia* from Nicaragua and Mexico. Vein 1 of the left primary runs along the bottom of each photograph. 1, Holotype of *ovina*, Nicaragua (BMNH). 2, Las Delicias, Chiapas, 8 August 1975, P. Hubbell (AMNH). 3, Holotype of *zaovinia*, Tehuacan, Puebla, August 1911, R. Müller (USNM). 4, Acahuizotla, Guerrero, August 1958, T. Escalante (AMNH). 5, Mexcala, Guerrero, August 1960, T. Escalante (AME).

much narrower at the base so that, even though it does taper toward the apex, it is more nearly oblong in outline (Figs. 41, 42, 44-47). In *edwardsi*, the lamella postvaginalis is broader—usually much broader—at the base and therefore much more triangular overall (Figs. 43, 48-55); together with its stalk, it sometimes suggests the stylized spearhead symbolizing spades on playing cards.



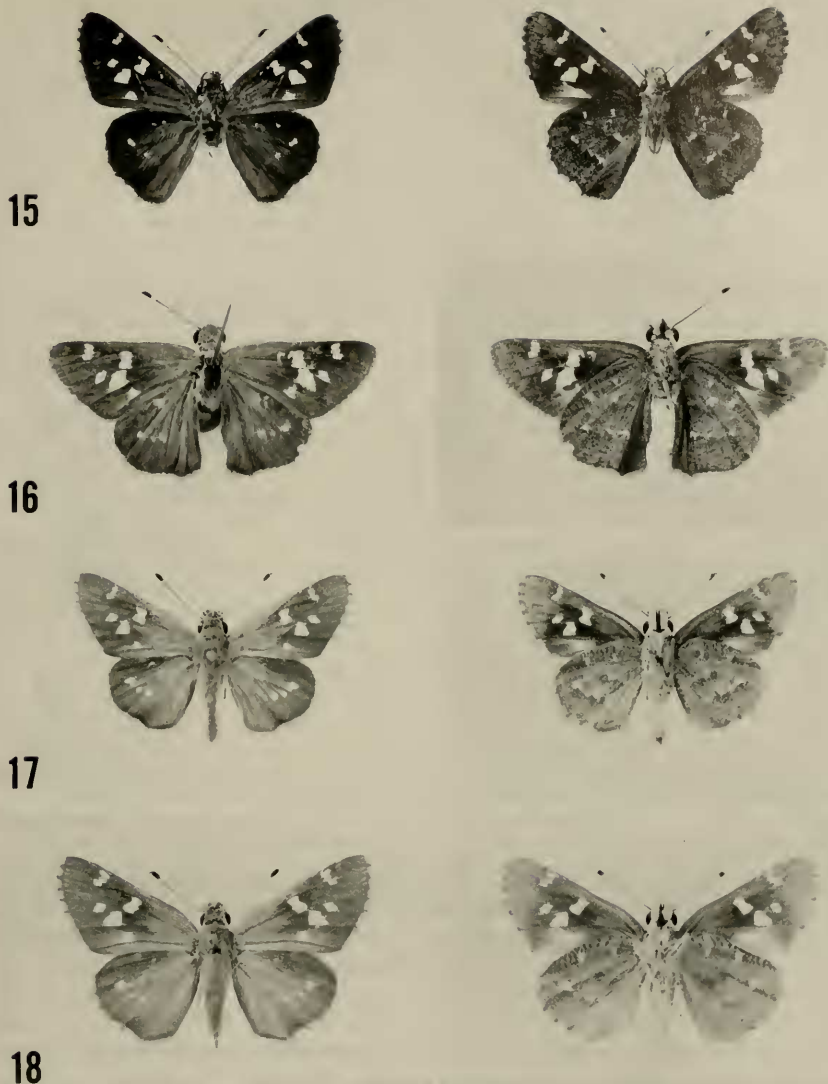
Figs. 6–10. Male stigmas of *Atrytonopsis edwardsi* from the United States and Mexico. Vein 1 of the left primary runs along the bottom of each photograph. 6, Lectotype of *edwardsi*, “Redington” (probably Santa Catalina Mountains), Arizona (USNM). 7, Limpia Canyon, 1465 m, Davis Mountains, 1.6 km N Ft. Davis, Jeff Davis County, Texas, 1 May 1959, J. M. and S. N. Burns (USNM). 8, Baboquivari Mountains, Pima County, Arizona (USNM). 9, Presidio, Veracruz, June 1942, T. Escalante (AME). 10, Ajijic, Jalisco, 3 September 1966, R. Wind (AMNH).

In superspecies *A. ovinia*, the lamella postvaginalis is so elongate that its distal end, like the end of the uncus, often protrudes enough to show without dissection. Unfortunately, one can rarely see all the way to the base, which is crucial for species discrimination.



Figs. 11–14. Type-specimens relating to superspecies *Atrytonopsis ovinia*, dorsal and ventral view (all $\times 1$). 11, Holotype δ of *ovina*, Nicaragua (BMNH). 12, Holotype δ of *zaovinia*, Tehuacan, Mexico (USNM). 13, Lectotype δ of *edwardsi*, "Redington," Arizona (USNM). 14, Phony "type" ♀ of *rupilius*, Guadalajara, Mexico (USNM). 11 and 12 belong to *A. ovinia*; 13 and 14, to *A. edwardsi*.

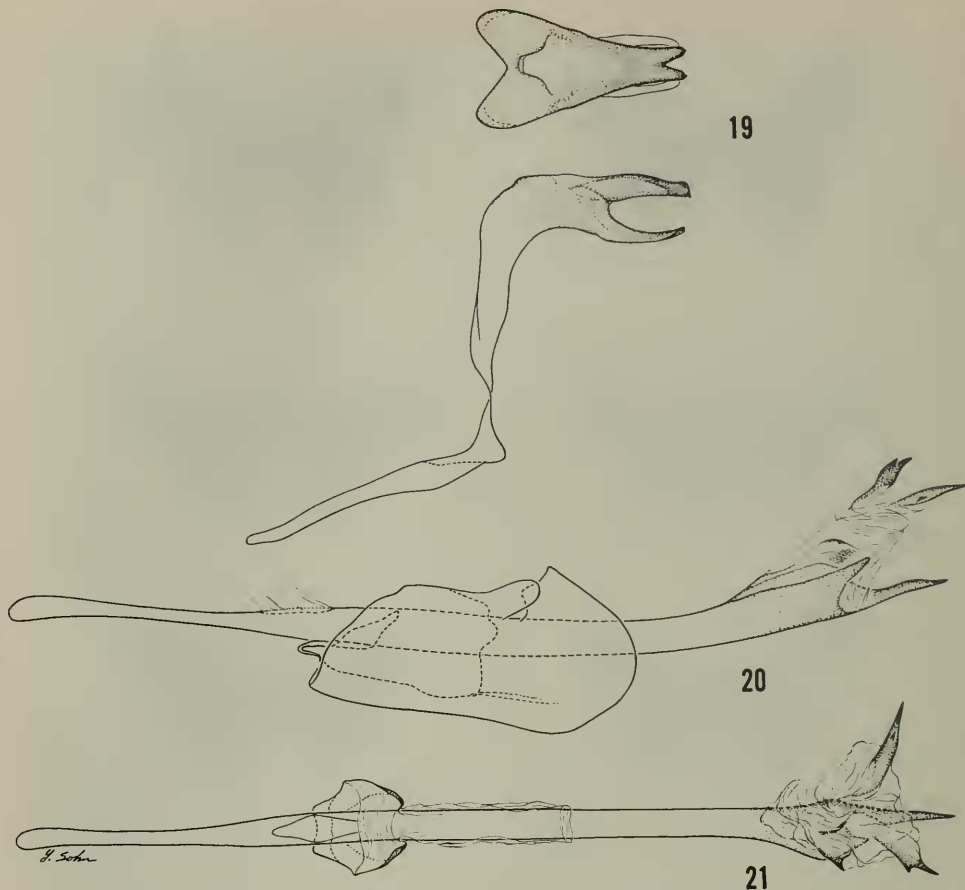
Temporal distribution.—Both members of superspecies *A. ovinia* are multi-voltine. Of the 31 dated Mexican specimens of *ovina* examined, 25 are from July and August; but the remaining 6 are from February, March, June, September, and December, which suggests that this southern species may fly in any month. The records may be concentrated in midsummer simply because most collecting is done then. Of the 261 specimens of *edwardsi* examined, 202 are dated and all



Figs. 15–18. Superspecies *Atrytonopsis ovinia*, dorsal and ventral view (all $\times 1$). 15, *A. ovinia*, ♂, Las Delicias, Chiapas, 8 August 1975, P. Hubbell (AMNH). 16, *A. ovinia*, ♀, Nicaragua (BMNH). 17–18, *A. edwardsi*, Limpia Canyon, 1525 m, Davis Mountains, 6.4 km WNW Ft. Davis, Jeff Davis County, Texas, 1 May 1959, J. M. and S. N. Burns (USNM). 17, ♂. 18, ♀.

but 3 of these are from the United States. The distribution of dates indicates two generations, with adults in spring (variously from March to June) and again in summer to about the beginning of fall (July to September). The second generation is smaller than the first.

Spatial distribution.—Superspecies *A. ovinia* occurs discontinuously from the southwestern United States to central Central America. Its “known” southern



Figs. 19–21. Male genitalia of holotype of *Atrytonopsis ovinia* from Nicaragua (X-1296) (BMNH). 19, Uncus, gnathos, and tegumen in dorsal view and uncus, gnathos, tegumen, vinculum, and saccus in left lateral view. 20, Left valva, aedeagus, and juxta in left lateral view. 21, Aedeagus and juxta in dorsal view.

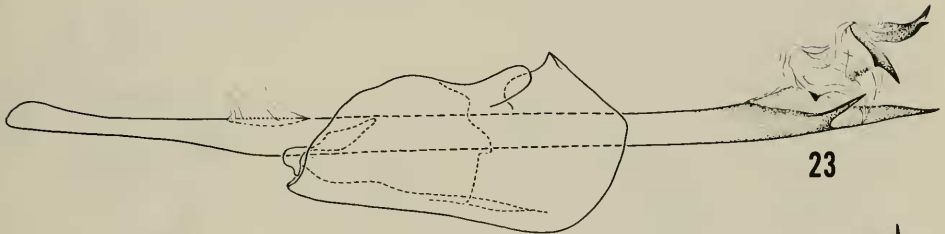
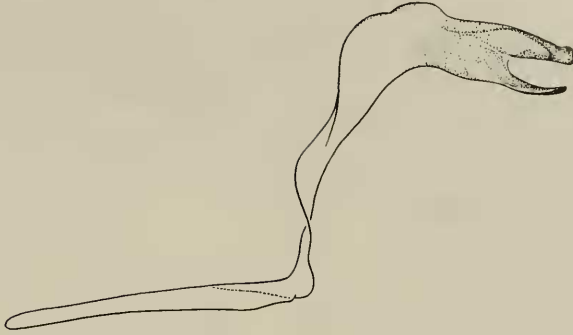
limit is somewhere in Nicaragua, at least, and probably farther south in north-eastern Costa Rica around Guapiles (the source of *rupilius*, according to Schaus; see discussion in Nomenclature and synonymy, above).

The more northern *edwardsi* ranges from the mountain islands of southeastern Arizona (plus immediately adjacent southwestern New Mexico) and those of Trans-Pecos Texas south primarily via the Sierra Madre Occidental and Oriental to Jalisco and Veracruz and the transverse Volcanic Cordillera (Fig. 56). It occurs at lower middle elevations from 850 to 1830 m (2800–6000 ft), but especially from 1220 to 1525 m (4000–5000 ft), and favors rocky canyons in foothill situations from the upper edge of desert, through grassland, to the lower edge of open oak woodland.

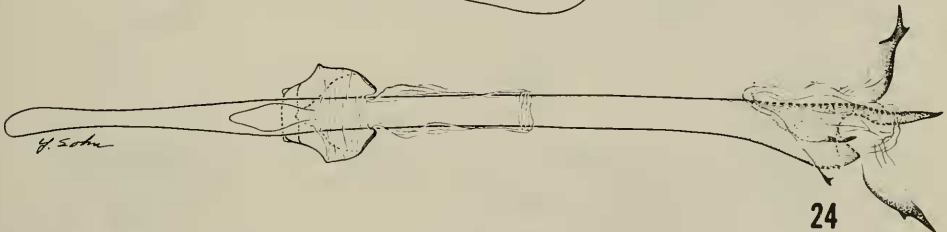
Unexpectedly, the more southern *ovinia* occurs at lower, rather than higher, elevations: points from 550 to 750 m (1800–2460 ft) have been recorded (though the real spread is wider). In Mexico, *ovinia* ranges from Guerrero and southern



22



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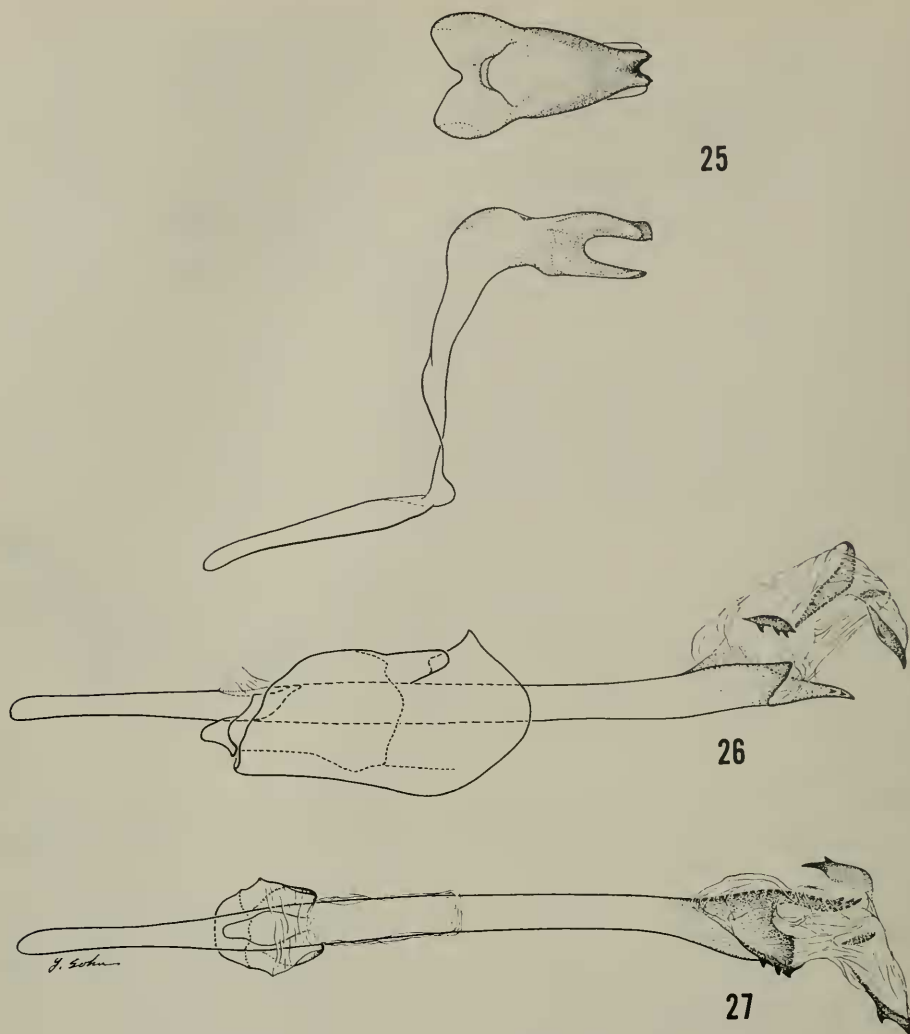


24

Figs. 22-24. Male genitalia of holotype of *Atrytonopsis zaovinia* from Tehuacan, Mexico, August 1911, R. Müller (X-1061) (USNM). 22, Uncus, gnathos, and tegumen in dorsal view and uncus, gnathos, tegumen, vinculum, and saccus in left lateral view. 23, Left valva, aedeagus, and juxta in left lateral view. 24, Aedeagus and juxta in dorsal view.

Puebla (Tehuacan) through Oaxaca and Chiapas and nips the southern edge of Tabasco (Teapa) (Fig. 56). It seems to favor dry, rocky (sometimes limestone) country supporting seasonally dry scrub or thorn forest (L. D. Miller and P. Hubbell, personal communications 1982). It must occur in Guatemala, Honduras, and El Salvador: on the one hand, specimens have been taken at two spots close to the Guatemalan border in the Chiapas Highlands (which continue into Guatemala); on the other, three specimens are known from Nicaragua, and one has been reported from northeastern Costa Rica.

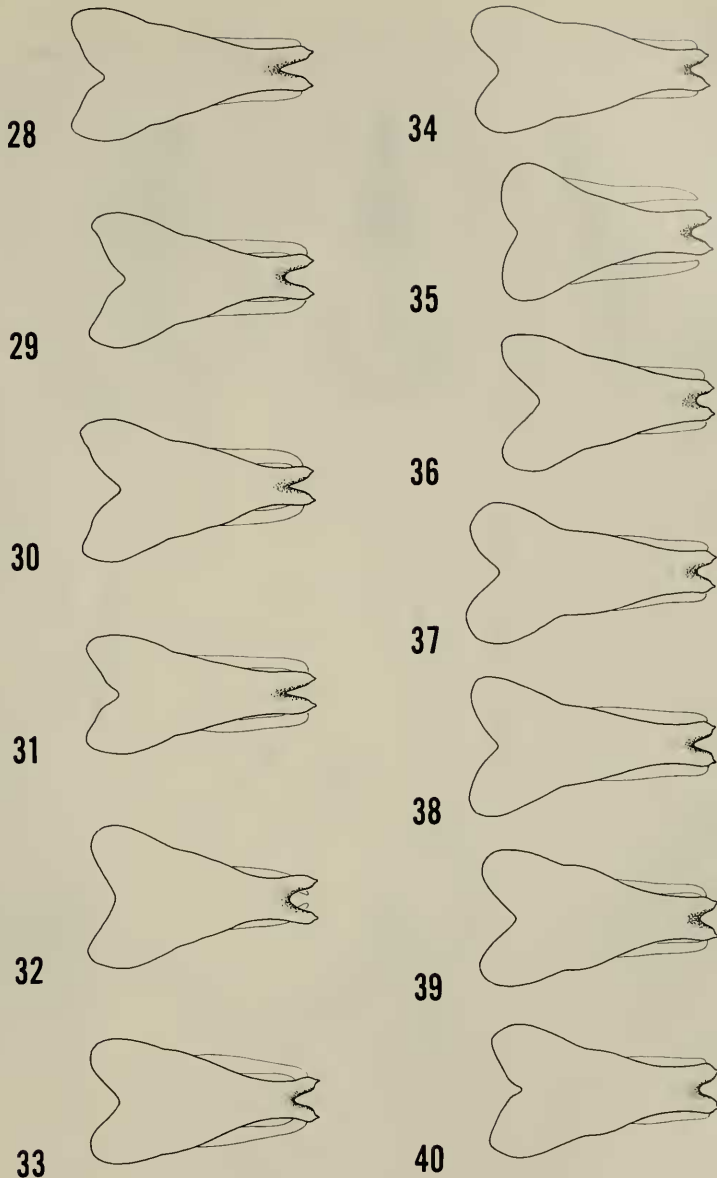
Atrytonopsis ovinia and *edwardsi* appear to be allopatric (there are too few Mexican records to state flatly that these species neither meet nor overlap a little). In general, they are altitudinally displaced. Although elevation is lacking, the specimen of *ovinia* labelled Teapa presumably comes from as low as 300 m (1000



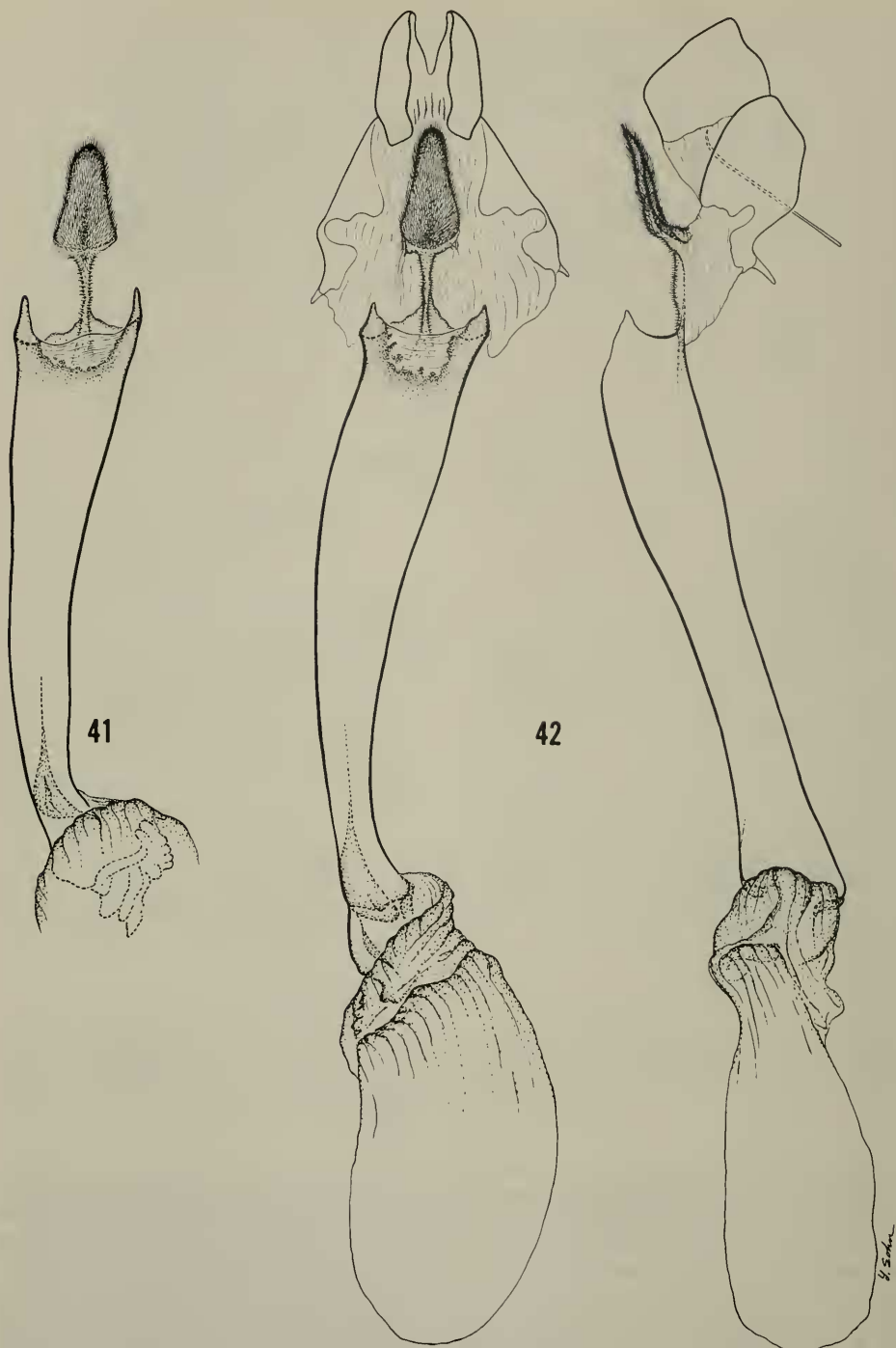
Figs. 25–27. Male genitalia of lectotype of *Atrytonopsis edwardsi* from “Redington” (probably Santa Catalina Mountains), Arizona (X-1295) (USNM). 25, Uncus, gnathos, and tegumen in dorsal view and uncus, gnathos, tegumen, vinculum, and saccus in left lateral view. 26, Left valva, aedeagus, and juxta in left lateral view. 27, Aedeagus and juxta in dorsal view.

ft) or lower; and only the specimens of *ovinia* labelled Tehuacan would seem to be as high as the preferred elevational range of *edwardsi*.

Where *ovinia* and *edwardsi* are closest to each other (Fig. 56), the dot marks Tehuacan, Puebla, and the triangle, Presidio, Veracruz. “Presidio” is the one name that still gave me some latitude when I started plotting symbols: it occurs twice in Veracruz, not only as a larger, more familiar railroad community 28 km southeast of Cordoba, cited in the *Biologia Centrali-Americana* and pinpointed by Selander and Vaurie (1962: 46), but also as a village 20 km north-northwest of Cordoba. I chose the latter because it lies in the pine-oak zone, between 915



Figs. 28–40. Uncus, gnathos, and tegumen of the male genitalia of superspecies *Atrytonopsis ovinia* in dorsal view. 28–33, *A. ovinia* from Mexico. 34–40, *A. edwardsi* from the United States and Mexico. 28, Guerrero, July 1920, R. Müller (X-1057) (USNM). 29, Mexcala, 550 m, Guerrero, 22 July 1956, K. Wilson (X-1066) (AMNH). 30–31, Tehuacan, Puebla, 14 August 1964, H. A. Freeman (X-1064 and 1065) (AMNH). 32, Teapa, Tabasco, December 1912, R. Müller (X-1068) (USNM). 33, Las Delicias, Chiapas, 8 August 1975, P. Hubbell (X-1067) (AMNH). 34–36, Baboquivari Mountains, Pima County, Arizona, 1 to 15 June 1924, 1 to 15 July 1924, and 1924, O. C. Poling (X-1150, 1072, and 1147) (USNM). 37, ca. 29 km W Cananea, Sonora, 26 August 1969, P. Hubbell (X-1069) (AMNH). 38, Limpia Canyon, 1525 m, Davis Mountains, 6.4 km WNW Ft. Davis, Jeff Davis County, Texas, 1 May 1959, J. M. and S. N. Burns (X-1300) (USNM). 39, 3.2 km N Shafter, Presidio County, Texas, 28 May 1973, W. W. McGuire (X-1071) (USNM). 40, Ajijic, Jalisco, 3 September 1966, R. Wind (X-1070) (AMNH).



Figs. 41-42. Female genitalia of *Atrytonopsis ovinia* from extremes of the known geographic range. 41, Lamella postvaginalis, ostium bursae, and ductus bursae in ventral view. Tehuacan, Puebla, 14 August 1964, H. A. Freeman (X-1063) (AMNH). 42, Bursa copulatrix and tip of abdomen in ventral and right lateral view. Nicaragua (X-1297) (BMNH).

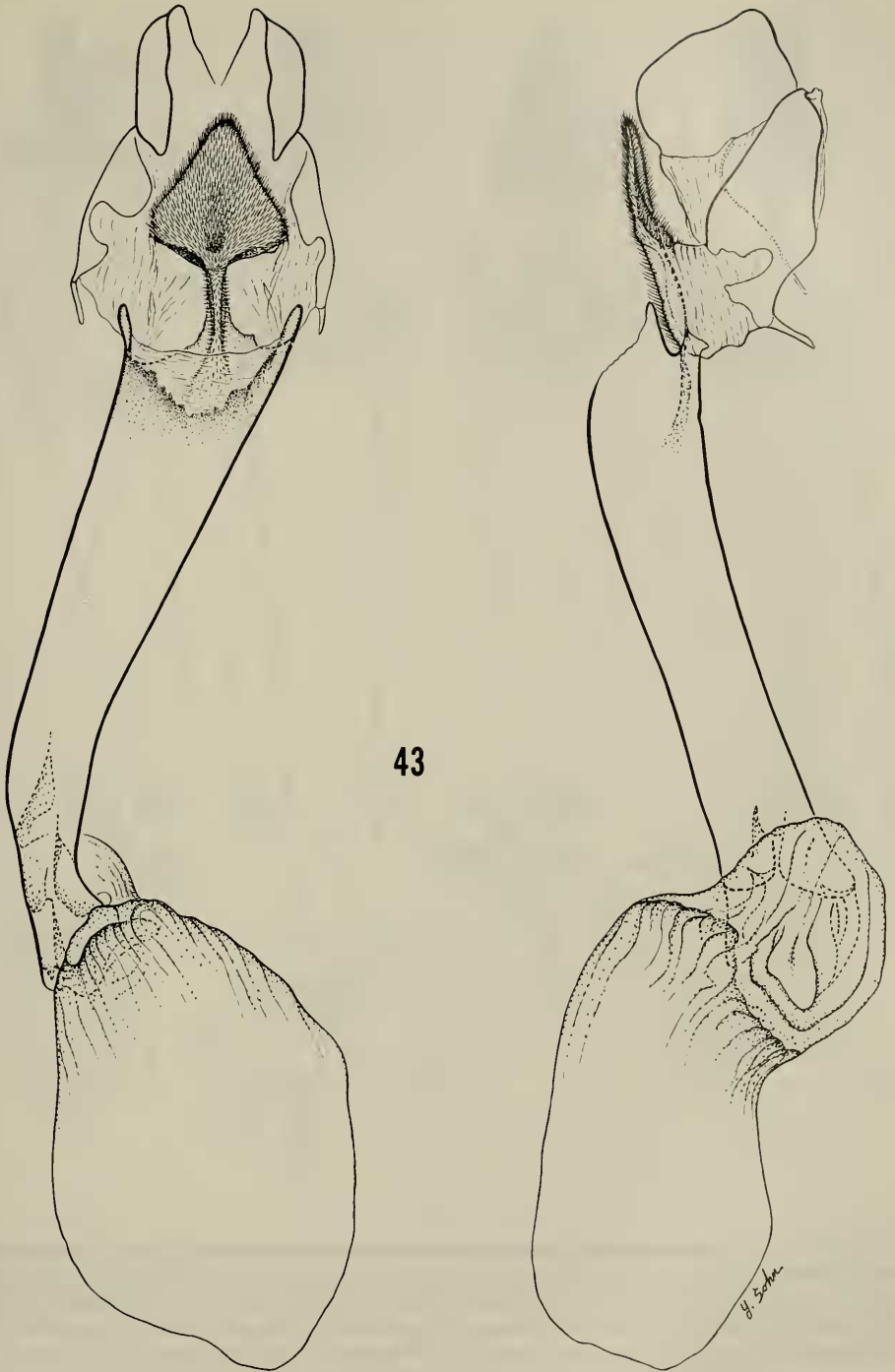
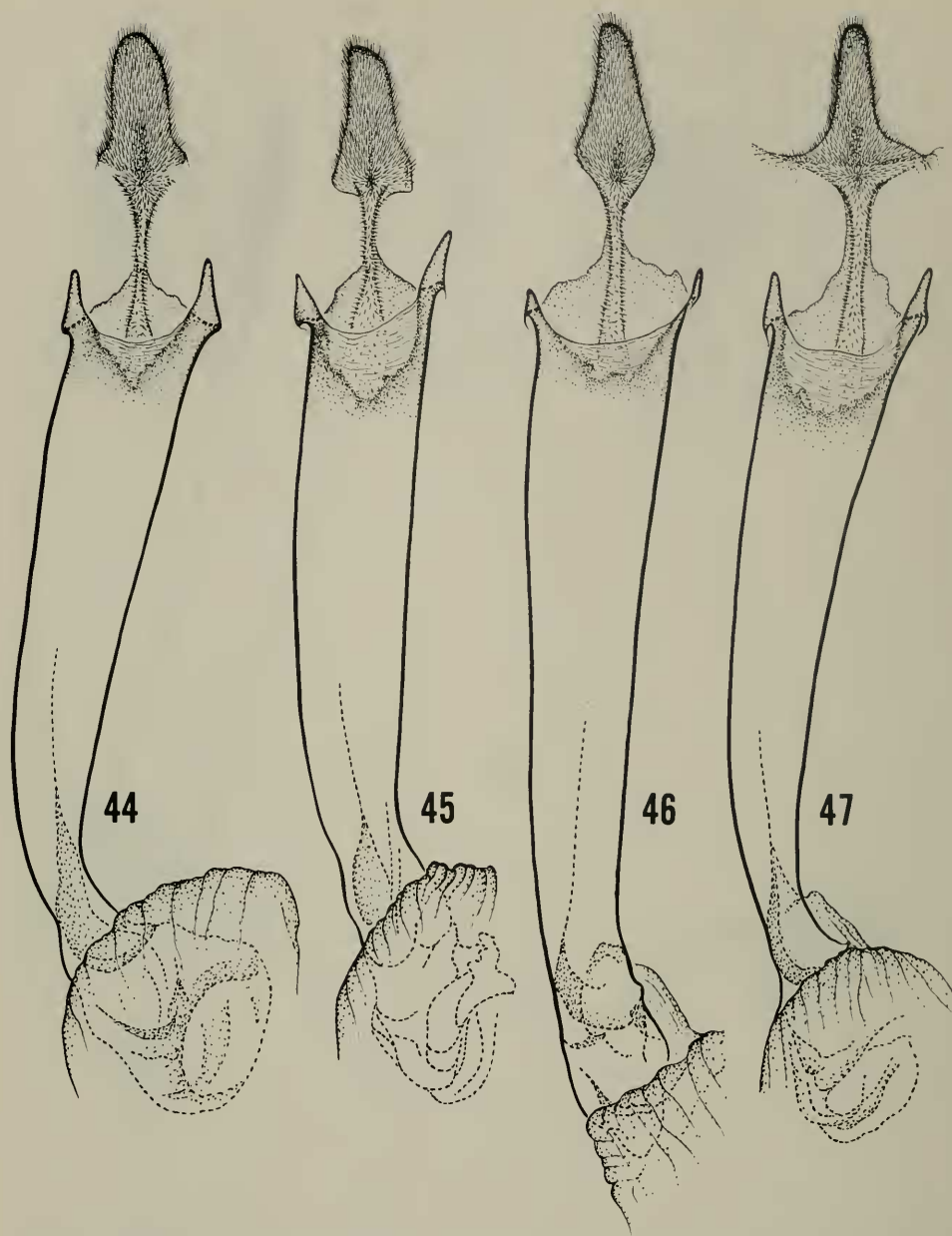
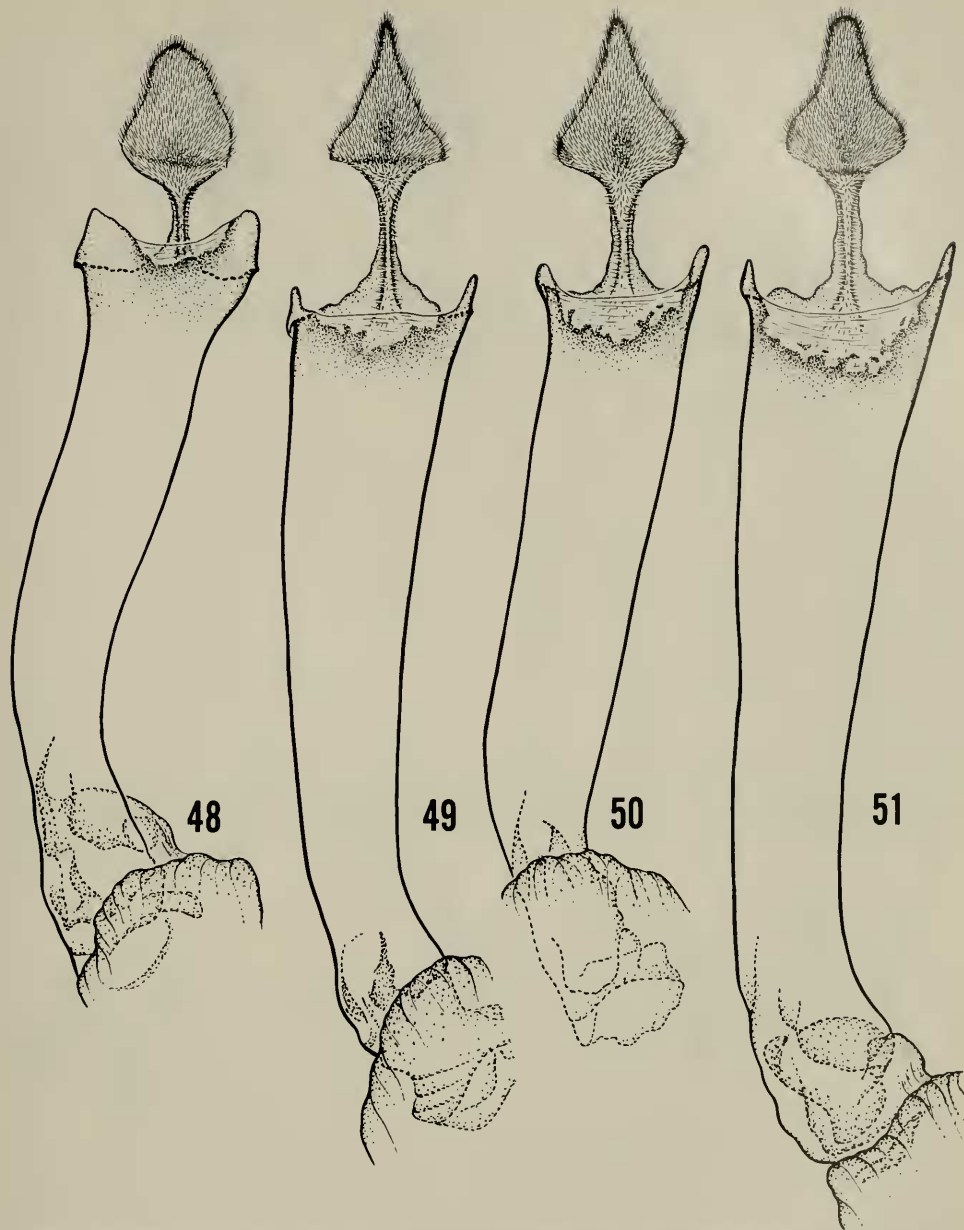


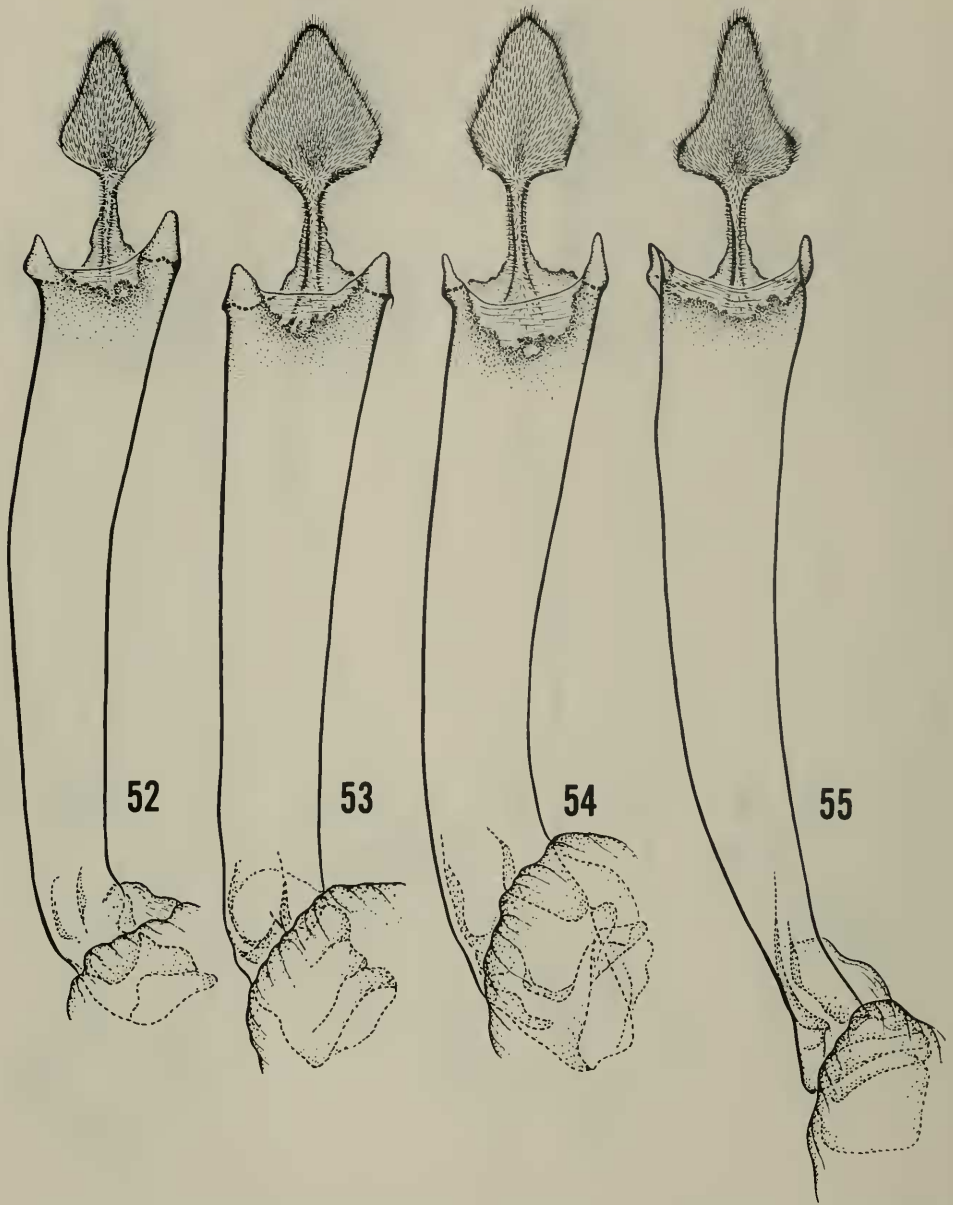
Fig. 43. Female genitalia of *Atrytonopsis edwardsi*. Bursa copulatrix and tip of abdomen in ventral and right lateral view. Limpia Canyon, 1525 m, Davis Mountains, 6.4 km WNW Ft. Davis, Jeff Davis County, Texas, 1 May 1959, J. M. and S. N. Burns (X-1309) (USNM).



Figs. 44-47. Female genitalia of *Atrytonopsis ovinia* from southern Mexico. Lamella postvaginalis, ostium bursae, and ductus bursae in ventral view. 44, Acahuizotla, Guerrero, June 1956, T. Escalante (X-1314) (AME). 45, 19 km E El Camaron, Oaxaca, 7 August 1956, J. W. MacSwain (X-1318) (MacNeill). 46, 32 km E El Camaron, Oaxaca, 20 July 1956, D. D. Linsdale (X-1317) (MacNeill). 47, Bombana, Chiapas, 12 to 18 September 1975, P. Hubbell (X-1319) (MacNeill).



Figs. 48–51. Female genitalia of *Atrytonopsis edwardsi* from the southwestern United States and central Mexico (all USNM). Lamella postvaginalis, ostium bursae, and ductus bursae in ventral view. 48, Limpia Canyon, 1435 m, Davis Mountains, 8 km NE Ft. Davis, Jeff Davis County, Texas, 4 May 1959, J. M. and S. N. Burns (X-1302). 49, Limpia Canyon, 1525 m, Davis Mountains, 6.4 km WNW Ft. Davis, Jeff Davis County, Texas, 1 May 1959, J. M. and S. N. Burns (X-1301). 50, “Redington,” Arizona (X-1075). 51, Guadalajara, Jalisco (X-1060)—the phony “type” of *rupilius*.



Figs. 52-55. Individual variation in female genitalia of *Atrytonopsis edwardsi* from the Baboquivari Mountains, Pima County, Arizona (all O. C. Poling, all USNM). 52, Brown's Canyon, ca. 1525 m, 1 to 15 June 1923 (X-1151). 53-54, 1 to 15 June 1924 (X-1074 and 1149). 55, 1 to 15 June 1923 (X-1042).

and 1525 m (3000 and 5000 ft); *edwardsi* has no business hanging around a railroad station in tropical lowland of about 300 m (1000 ft).

With so few Mexican records, it is worth mentioning a pair of *edwardsi* taken at Hermosillo in central Sonora on 20 October 1961 and reported by Miller (1970: 195), following Evans (1955: 386), as *A. ovinia zaovina*.

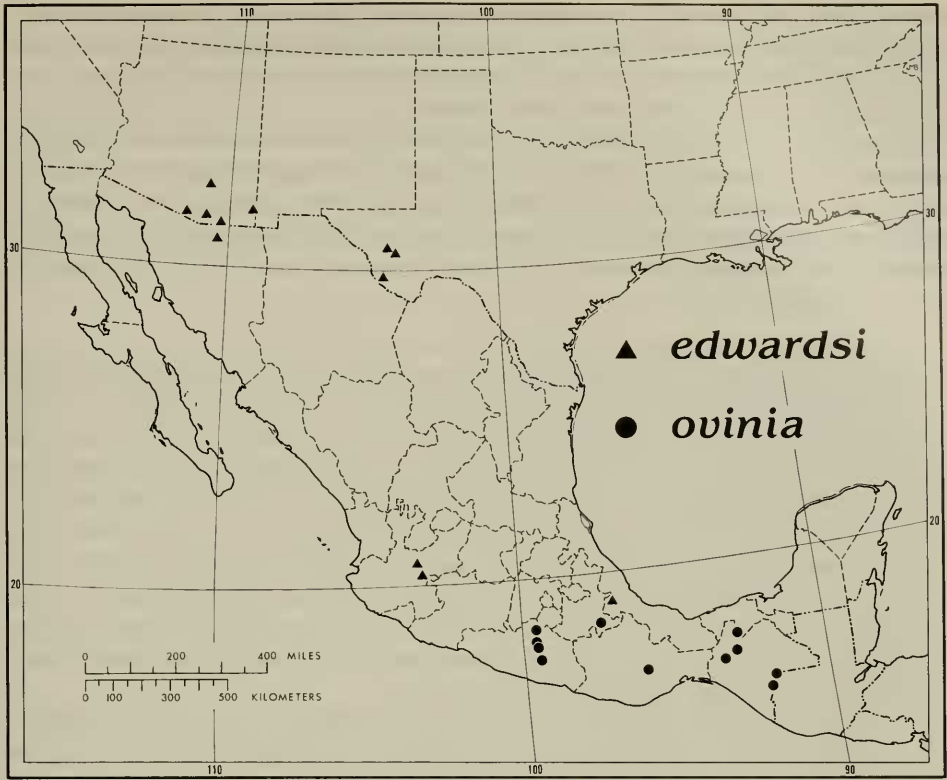


Fig. 56. Geographic distribution of superspecies *Atrytonopsis ovinia* (based on material examined). *Atrytonopsis ovinia* certainly extends to somewhere in Nicaragua, the type-locality, and probably to northeastern Costa Rica.

DISCUSSION

The gross morphologic characters that reliably separate *ovina* from *edwardsi* are secondary sex characters: the stigma of the male and the genitalia of both sexes. In many sorts of organisms, it is structures like these that change most readily in the process of speciation.

Is such differentiation directly selected, or is it a more or less fortuitous result of other genetic reorganization associated with speciation? In both males and females, the genitalic differences between *ovina* and *edwardsi* are small—so small, in fact, and so variable, that their potential value in reproductively isolating these forms from one another seems nil. At the same time, differences in the stigma (a structure thought to function in mate recognition) are greater and might constitute a significant isolating mechanism. A crucial point, however, is that *ovina* and *edwardsi* appear to have arisen allopatrically and to have remained allopatric ever since. It is hard, then, to imagine any direct selection for the observed divergence in these characters. (They do not have to diverge, of course; note, e.g., the lack of differentiation in secondary sex characters among species of the *lunus* group of *Atrytonopsis* [Burns, 1982].) There may be a widespread, genetically based tendency for secondary sex characters to alter in the course of a genetic shake-up occurring in, say, the classic, initially small, (peripherally) isolated population of

Mayr (1954); but this would not be the same as selection directly effecting change. Although sympatric congeners of a speciating population might offer some constraints, selective pressure on secondary sex characters is more likely to come from secondary contact between sister species.

To rephrase the central idea, much of the interspecific morphologic variation (especially in genitalia) that I find so useful as a taxonomist strikes me as "noise" that does not harmonize with the dominant all-is-selected evolutionary theme. I was forced to similar conclusions more than two decades ago when I analyzed evolution in American species of *Erynnis* in detail (Burns, 1964: 4–6 [*italics* in third paragraph added]):

To determine specimens of *Erynnis* accurately, it is desirable, and often necessary, to examine their genitalia. The taxonomic value of the male genitalia has been known since Scudder and Burgess (1870) demonstrated the striking asymmetry that pervades these structures; but few workers have taken the trouble to use them. Comparable characters for identifying females have never been worked out. Since the sclerotized aedeagus of the male is, in various species, bent at an angle or oriented off the median dorsoventral plane, or both, the ostium bursae of the corresponding female is asymmetrically placed. The position of the ostium bursae, chiefly with respect to the midventral line (but also relative to the anterior and posterior limits of the sterigma), the form of the opening and adjacent heavy sclerotization, and the form of the sterigma together offer a set of reliable diagnostic characters. . . .

Members of genus *Erynnis* mate in a tandem, posterior-to-posterior position, and therefore an aedeagus directed toward a male's right requires an ostium bursae situated on the female's left. Since, in each sex, an asymmetrically placed organ sometimes lies on the left side, sometimes on the right (depending upon the species), crossing between certain species seems to be mechanically impossible. However, such incompatible species are always phylogenetically distant, whereas those that are closely related are similar to one another in genitalic structure. And in several species, both related and unrelated, aedeagus and ostium bursae lie in, or virtually in, the midline. Hence, asymmetry of these organs can scarcely have evolved as an isolating mechanism of a "lock-and-key" sort. (Among the criteria that I have used in relating species are within-sex similarities in genitalic structure; but because other characters—of which the most convincing is geographic distribution—have simultaneously been considered, the conclusion stated above does not really rest on a circular argument.) . . .

The bizarre configurations and spinose surfaces of the male genitalia suggest an ethologic role involving exchange of tactile stimuli (perhaps in ordered sequence) between male and female in the initial phases of copulation. *Yet it is doubtful that the differing genitalic structure of different species has arisen other than accidentally, or that, once having arisen, it has gained selective advantage by promoting behavioral reproductive isolation; genitalic asymmetry is exceptional in skippers, and among many of them—notably hesperiines—male genitalia may be extremely similar in form throughout a genus. In Erynnis, no genitalic differences mark some closely related species that are partly sympatric (E. lucilius and E. baptisiae) or at least contiguous (E. zarucco and E. funeralis),*

while extensive and more or less constant genitalic differences distinguish males of some other closely related forms that are allopatric and contiguous (e.g., *E. horatius* vs. *E. tristis*; *E. brizo brizo* vs. *E. brizo burgessi*) or even widely separated by stretches of uninhabitable terrain (e.g., *E. propertius* vs. *E. meridianus*; *E. b. burgessi* vs. *E. b. lacustra*). Species of *Erynnis* with which these forms are broadly sympatric are thought to be sufficiently unrelated to preclude interspecific sexual interest beyond that which is merely tentative and investigatory. *It would appear, then, that the genitalic differences are simply an aspect of general differentiation and divergence undergone by geographically isolated populations.*

Earlier, in reviewing the evolution of mimetic polymorphism in Lepidoptera, I leaned toward a flexible Goldschmidtian approach that considered genetics-and-development (as well as selection) and away from the rigid, excruciatingly cumulative micro selectionism of Fisher and Ford (Burns, 1956: 80–82). Sweeping criticism has lately been leveled at Anglo-American evolutionary biologists of the last forty-odd years for ascribing too much evolutionary change to direct selection (and attendant tight adaptation), as if organisms really were reducible to discrete characters and, therefore, less than integrated wholes (Gould and Lewontin, 1979).

In both *ovinia* and *edwardsi*, the stigma and the male and female genitalia (plus other characters studied) show a lot of individual variation (some of which I have tried to convey in figures) but no detectable geographic variation, even though the range of each species is highly discontinuous. Despite the individual variation, the subtle interspecific differences in genitalia are perceptible throughout the known range of each species. This essential “uniformity” through each sister species suggests differentiation in a small isolate followed by dispersal and expansion of range without further important genetic change, an interpretation consistent with a punctuational model of speciation.

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